Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

POST-GLACIAL NEARCTIC CENTRES OF DISPERSAL FOR REPTILES.

BY ARTHUR ERWIN BROWN.

If lasting values are to be reached in the study of geographical distribution, its conclusions must accord with all else that is known of the dynamics of evolution. Or, stated with more exact reference to its especial problems, the areas marked off by it must correspond to the distributional relations of genetically connected species and, at the least, must not be at fault with possible lines of dispersal from centres of development by which they may have come to occupy their present range. What is proposed here is an attempt to determine such centres for *Reptilia* in North America.

The scarcity of Tertiary remains of reptiles belonging to existing groups confines the student of geographical distribution in the main to post-glacial conditions, with little more knowledge of those preceding than the practical certainty that genera now widely ranging are of great antiquity and were likewise wide ranging in earlier periods, and that a former north Atlantic land connection between Europe and America must have coincided with a climate of sufficient warmth to serve for the passage of reptiles belonging to genera now common to both.

In other ways the problem is simplified by the absence in later periods of a circumpolar reptilian fauna, a consequence of which is that the chief zoological bond of connection between the eastern and western continents is wanting, and for reptiles a "Holarctic" region or an "Arctogæan" realm can not be said to exist, the families and genera common to more southern portions of both being insufficient to link them. For this reason Mr. Sclater's term "Nearctic" is used here. It should be said, however, that if for purposes of convenience or uniformity it be desired to retain these later and broader generalizations, no harm is likely to ensue if it be remembered that they do not express the exact facts of present reptilian distribution, whatever they may have been during the Tertiary.

A further simplification results in northern regions from this same absence of boreal reptiles, for it eliminates the meeting ground of a northern with a southern migration, which constitutes the "Transition" zone of various authors in other groups. If a transition zone existed in the Nearctic for reptiles it would follow meridians of longitude west of the Mississippi river, instead of extending from east to west.

I have stated elsewhere[1] that the present distribution of Nearctic reptiles points to the two post-glacial centres indicated by Prof. C. C. Adams,[2] one in the southeastern Austroriparian, the other southwestern, in the Sonoran. Some space must now be given to the evidence.

In the same paper it was shown that in the southern Nearctic the eastern and western reptilian faunas are so distinct that the community between them is limited to a few species belonging to widely ranging genera, and that the zone of change between them lies approximately between the 96° and 98° meridians of longitude in Texas. In a general way this zone may be carried north along those meridians, to mark the separation between the whole Atlantic and the whole Sonoran faunas, widening, however, toward the north in following up the rivers of the Mississippi drainage.

The division is in some measure obscured by the presence in the lowlands of the Mississippi and its tributaries of a few species, chiefly serpents, originally derived from both faunas and occupying the contiguous portions of their respective areas.

The proposition that original post-glacial centres must have lain far to the south, is more logically necessary in the case of reptiles than with other vertebrates, and follows from their dependence as a class upon warmth. If further evidence were needed, it would be found in their great numerical superiority, both in species and individuals, in the south. The whole extent of North America reaching from the border of the great plains eastward to the Atlantic coast, and from the Gulf of Mexico to the northern limit of reptiles, which, following Agassiz, will here be known as the Atlantic subregion, to avoid confusion with its Eastern district, contains 113 species and recognizable subspecies in all orders of reptiles. Of these 56 are confined to some portion of the Austroriparian district, and 15 are exclusively Eastern, with 42 common to both, practically all of which are southern intrusions to varying distances into the Eastern. In the western Nearctic the distribution of species is vastly more complex as to its details, on account of the great variety of surrounding conditions in contiguous areas produced by rapid changes in altitude, and is not yet fully known, but the excess of southern species is even greater, for assuming that Dr. Merriam's division of the country from the western border of the

---

[1] *Proc. Acad. Nat. Sci. of Phila.*, 1903, p. 551.

[2] *Biological Bulletin*, Vol. III, p. 121 (1902).

Atlantic subregion to the Pacific coast into a Lower and an Upper Sonoran accords best with present knowledge, the Lower Sonoran seems to have about 74 peculiar species, and the Upper Sonoran plus his Transition has but about 13, with 35 common to both, of which 19 may be regarded as Lower Sonoran and only 6 as Upper. The remainder belong to the Atlantic fauna. It should be explained that these estimates are based upon a somewhat conservative view as to species, but if the method of minute analysis characteristic of the present time be followed, the predominance of Lower Sonoran forms will be even greater.

Both from the logical necessity of the case and from the application of one of the main criteria in common use, it seems clear that the areas which at the retreat of the ice contained the elements from which our present reptilian fauna has developed, must be sought for in the south.

The briefest examination of the character and the abounding richness of the reptiles inhabiting the dry plateau extending from Texas to Arizona and south into Mexico, as well as the physical geography of the whole Sonoran subregion, are enough to show that the dispersal centre of that fauna was here, in Cope's Chihuahuan.

The Austroriparian is less clear without close examination of evidence. Two localities in this subregion excel all others in variety of species, one in the extreme southeast toward Georgia and Florida, corresponding to the fauna termed by Cope *Ocmulgian;* the other, or *Louisianan,* on the lower Mississippi. Fifty-one species are common to both, and in addition the Ocmulgian, including Cope's *Floridan,* presents 21 not extending into the Louisianan, which in turn has 14, one half of them, however, only entering its western border from the Sonoran. Of the two the Ocmulgian shows a decidedly greater diversity in species.

A study in some detail of the genera points in the same direction. Little argument is required to demonstrate the proposition that genera now common to the Nearctic and the western Palæarctic must have had that range established at a time when a Tertiary north Atlantic land connection coincided with a warm climate in the north, for the absence from all beyond the northern border of the Neotropical of such vigorous Nearctic genera as *Coluber, Zamenis, Tropidonotus, Eutænia, Ophibolus* and others, which are identical with or nearly related to Holarctic genera, renders it impossible that such community in northern regions could have come about by means of the Antarctic continent whose former existence is now urged by many palæontologists, however well this would serve to explain such anomalies as the presence of pleurodire turtles in South America, and of two genera of Neotropical Boidæ in Madagascar. It has been shown by Heer, in his researches upon Arctic fossil plants, that in the process of secular cooling the mean temperature of northern Greenland, as late as the early Miocene, was not far removed from that of central Virginia at the present time—quite warm enough for the needs of such hardy stocks as the genera above named—and the differentiation of reptiles of modern types had progressed so far by the close of the Mesozoic, that not much risk is incurred in believing that many existing genera were in existence long before the end of the Eocene. Assuming a north Atlantic highroad to have been the means of communication, the longest Nearctic establishment of these common forms is likely to have been in the older geological regions far in the east. It is further true that with many of them traces of their primitive representatives appear to be found in existing species of the eastern part of the Austroriparian.

Omitting mere Neotropical intrusions into the southern border of the Nearctic, such as *Alligator, Crocodilus, Anolis, Sphærodactylus, Helicops, Spilotes, Rhadinea, Drymobius, Tantilla, Erythrolamprus* and *Elaps,* as well as *Trionyx, Chelydra, Emys* and *Testudo,* each of which had a wide Tertiary extension in northern regions, but whose recent distribution throws no further light on the present question, most of the remaining genera may be referred for their origin to the Austroriparian or Lower Sonoran faunas.

Austroriparian:

Macroclemmys
Aromochelys
Cinosternum
Chrysemys
Malaclemmys
Terrapene
Ophisaurus
Liolepisma
Rhineura
Eutænia
Tropidonotus
Seminatrix
Storeria
Clonophis
Tropidoclonium
Haldea
Amphiardis
Coluber
Zamenis
Cyclophis
Liopeltis
Diadophis
Ophibolus
Stilosoma
Carphophis
Farancia
Abastor
Virginia
Cemophora
Heterodon
Ancistrodon

Lower Sonoran:

Ctenosaura
Dipsosaurus
Crotaphytus
Sauromalus
Callisaurus
Uma
Holbrookia
Uta
Sceloporus
Phrynosoma
Eublepharis
Heloderma
Gerrhonotus
Xantusia
Verticaria
Cnemidophorus
Eumeces
Anniella
Glauconia
Lichanura
Charina
Arizona
Pityophis
Salvadora
Phyllorhynchus
Contia
Ficimia
Chilomeniscus
Rhinochilus
Hypsiglena
Trimorphodon
Sibon
Sistrurus
Crotolus

In searching for the localities which may be conceived to have been those of the Nearctic origin of genera, it is to be observed that little is to be learned from Chelonia, for the aquatic habits of most of the order renders them relatively untrustworthy as guides in terrestrial distribution and, furthermore, we are as yet ignorant of the characters in most genera which should be regarded as primitive. Nevertheless, it is obvious that conditions best favoring the development of fresh-water turtles must have always been far more completely presented in the well watered Atlantic subregion than in the arid Sonoran.

In Cinosternidæ the extensive range of the Atlantic species, *Cinosternum pennsylvanicum* and *Aromochelys odoratus*, favors the view that they have been longest established, and it would appear further that the Louisianan and Sonoran species do not exhibit any great amount of differentiation from these forms.

Of the thirteen species of *Chrysemys* found in the whole Nearctic, ten are restricted to the Atlantic subregion. Eight of these are Austroriparian, three of them entering the Eastern. The near relationship between *C. concinna*, *C. mobilensis*, *C. scabra* and *C. rubriventris*, all especially numerous on the southeastern coast, points to their long presence there.

In the Nearctic, *Emys* and *Clemmys* are confined to the Eastern, with the exception of one species of *Clemmys* on the Pacific coast, but each has a representative in the Palæarctic, and *Emys* is known from the Eocene of both continents. No reason can be assigned for their present limited Nearctic range, which must be looked upon as one of the anomalies of survival of ancient forms.

The box tortoises of the genus *Terrapene* range everywhere east of the Rocky mountains, but if the view of Dr. Baur be accepted, that the gradual disappearance of the quadrato-jugal is a progressive character, *T. major* of the southern Austroriparian and *T. bauri* of Florida are the most primitive.

A distinctly negative character of the whole Atlantic subregion is its poverty in lizards, their almost complete absence being, in fact, the correlative of an abundance of water turtles. Its lizards are Sonoran, with the exception of *Ophisaurus*, restricted to the Austroriparian, whose close relationship to the Palæarctic *Pseudopus* justifies placing its original centre along the Atlantic coast, and *Rhineura,* now only found in Florida, but perhaps known from the Oligocene of Dakota. *Liolepisma laterale,* which occupies only the Austroriparian and the southeastern corner of the Eastern as far as New Jersey, belongs to a genus of wide extension in the Australian, Ethiopian and Oriental regions, but having no other representative in the Holarctic except one in China, whose specific characters are identical with it.[3] This instance conforms to the unknown law which has preserved on the eastern shores of Asia and North America so many allied remnants of ancient groups among both animals and plants.

More exact evidence is afforded by Ophidia, for with two exceptions it is believed that the genera now widely spread in the Nearctic can be shown to have probably originated in the eastern centre. Of those more locally restricted, which must in most cases be descendants of these earlier forms, a difficulty must be admitted in the comparative absence of structural clues to relationship, especially in Colubridæ. The relative position assigned to genera by Mr. Boulenger, however, merits a high degree of confidence and has been much relied upon. It may be added that there are quite enough cases where high probability can be assured, to warrant propositions with which the uncertain ones at least fail to conflict.

The genus *Tropidonotus,* cosmopolitan as to the greater life areas except that it enters only the northern border of the Neotropical, in the Nearctic is absent from the Pacific coast, and in fact enters the Sonoran only by its river bottoms, from which the assumption is justified that it originally entered North America from western Europe. The common species of the whole Atlantic subregion, *Tropidonotus sipedon,* seems quite surely to have been near the parent form, though it is less clear which of the two subspecies, *T. s. sipedon* or *T. s. fasciatus,* should be regarded. The young of both, as a rule, have the color pattern of the adults, but more or less cross-banding with narrow interspaces frequently replaces the spots on the forepart of the body in young and some adult *T. s. sipedon,* resembling those which form the normal pattern on the whole length in eastern examples of *T. s. fasciatus*—a fact which perhaps signifies the partial retention of an ancestral pattern, now completely lost in the third subspecies, *T. s. transversus* of the Louisianan fauna. It is probable that *T. s. fasciatus* of the southeast represents the earliest form. Within the bounds of the Ocmulgian, *T. cyclopeum* and *T. taxispilotus* have developed from *T. sipedon,* while farther west, in the Mississippi valley, the way to *T. rhombifer* was through *T. s. transversus.* The whole of the ill-defined series grouped about *T. compressicaudus* and *T. ustus* is Floridan and shows the wealth of differentiation, still unstable as to fixity of character, which has resulted in the Ocmulgian under conditions highly favorable to the genus. There seems no clue to the direct origin of the group of species represented by *T. leberis* and its allies, with seventeen or nineteen rows of scales and longitudinal stripes, but it is worth noting that a similar distribution of color occurs in a number of eastern Palæarctic and Oriental *Tropidonotus.*

---

[3] Boulenger, *Cat. of Lizards,* Vol. III, p. 264.

Separated structurally from the foregoing genus only by its entire anal plate is *Eutœnia,* which covers the whole Nearctic to the northern limit of snakes, and perhaps equals in number of individuals all other species combined. From its cosmopolitan extension *Tropidonotus* must be the parent. It is suggestive that the eastern form of the common garter snake, known as *E. sirtalis ordinatus,* with dark spots on a greenish ground and no stripes, much resembles some color phases of *Tropidonotus natrix* of Europe, and has like it nineteen rows of scales and seven upper labials. The yellow collar of *T. natrix* is not known in any race of *E. sirtalis,* but it possibly reappears in the pale postoral crescents of some Sonoran species, as *E. marciana* and *E. hammondi.*

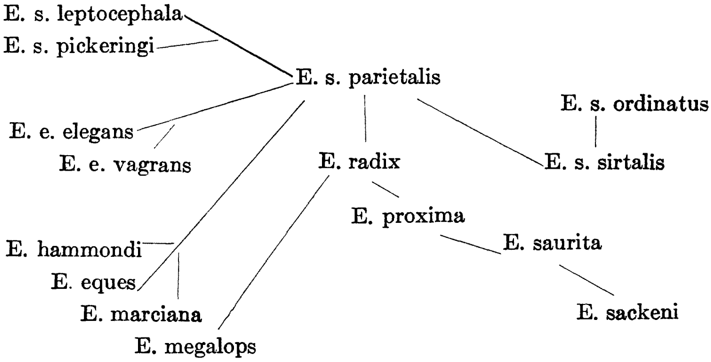
E. s. ordinatus grades into *E. s. sirtalis,* whose western representative, *E. s. parietalis,* on the Pacific coast runs into *E. elegans* through such examples as those which Cope regarded as *E. infernalis,*[4] and in the southwestern Sonoran into *E. marciana, E. hammondi* and *E. eques.*

The species of the great plains, *E. radix,* has commonly twenty-one scale rows and seven upper labials, but often presents the scutellation of *E. sirtalis* and probably is derived from it, an important change being that the lateral stripe has moved up one row of scales. And it is of interest here to note that certain garter snakes from Indiana, about the eastern limit of *E. radix*, called by Cope *E. butleri*, show irregularities in the position of the lateral stripe perhaps indicating transition. *E. radix* is a connecting link on the one hand with *E. proxima* of the Mississippi valley, which in the east has given off *E. saurita* and *E. sackeni*, and on the other, in the southwest with *E. megalops* and doubtles other Mexican forms.

---

[4] A. E. Brown, *Proc. Acad. Nat. Sci. of Phila.,* 1903, p. 288, etc.

If this hypothetical family-tree of *Eutænia* is correct, an interesting lesson in lines of dispersal of Austroriparian genera may be gained from their diagrammatic representation:



Of the remaining so-called Natricinæ, all of which are small and more or less degenerate representatives of *Tropidonotus* and *Eutænia* or of the stock from which they came, the most widely spread genera, *Storeria*, *Haldea* and *Virginia* are chiefly Atlantic, *Seminatrix* is wholly Ocmulgian, *Tropidoonium*, of limited range and probably of relatively late origin, belongs to the Mississippi valley, and the very few specimens of *Amphiardis* known are from Dallas, Texas, on the western borderland of the Austroriparian.

Among other widely ranging genera, *Zamenis* is an ancient form whose present distribution includes also the Palæarctic and Oriental regions. The earliest Nearctic style seems likely to be represented by *Z. flagellum flagellum*, which belongs to the Ocmulgian centre. The young of this species show narrow cross-bands, and occasionally much wider ones, as well as a tendency to form narrow stripes on the centres of some of the lateral scale rows, all of these being present as diagnostic characters in various combination in adults of most other American species. The inequality of color between the anterior and posterior portions of the body, characteristic of all, is most pronounced in *Z. f. flagellum*.

Coluber has about the same range as *Zamenis*, but in the Nearctic does not pass beyond the Rocky mountains. The distribution of color most common in the genus consists of three rows of spots, but in many species, especially in America, there is a disposition for these to run together by their corners and form longitudinal stripes. This is indicated more especially in some western and Central American species, as *C. subocularis* and *C. lineaticollis,* and culminates in *C. quadrivittatus,* which is spotted when young and wholly striped when mature. *C. obsoletus confinis* is in most respects generalized as to pattern, and either this species, or less probably *C. guttatus,* both chiefly Ocmulgian, are likely to be near the primitive form.

In the Lower Sonoran *Coluber* has given off *Arizona* and *Pityophis,* the last having sent one species, *P. melanoleucus,* the most specialized of the genus in the shape of its rostral, and in disappearance of the head bands in adults, back into the Atlantic as far north as New Jersey.

The genus *Ophibolus,* generally distributed in the Nearctic, except in the northwest, is nearly related to *Coronella* of the western Palæarctic and Ethiopian. It does not seem possible to determine whether the parent is represented by some color form of *O. getulus* or *O. doliatus,* but the coronelline affinity indicates with sufficient certainty that *Ophibolus* must have come from a source whose Palæarctic connections were by way of the eastern or north Atlantic route. It may be significant that while no subspecific distinction is warranted, most Floridan examples of *O. getulus getulus,* which is the most vigorous and extended species, seem to be rather generalized in the character of the dorsal spots and bands, as between northern specimens of the same form and the Louisianan *O. g. sayi.* The further fact has a bearing, that the specific characters of forms from the western part of the Nearctic seem to show less stability than the eastern ones, especially so in *O. g. boylii* and *O. g. californiæ,* thus pointing to a more recent development of these subspecies.

Liopeltis and *Cyclophis* are examples of the remarkable discontinuity already noted in the range of certain other genera common to eastern Asia and eastern North America. In the last *Liopeltis* covers the whole Atlantic subregion, while *Cyclophis* is mainly Austroriparian. Both extend to no great distance into the Sonoran.

The case for *Heterodon* is not free from doubt. The form of its rostral seems to suggest that it belongs among the types which have been so freely developed in the dry Lower Sonoran, and its possible relationship to the South American *Lystrophis* would accord with this assignment, but on the other hand, the largest and most widely spread species, *H. platyrhinos*, is found upon suitable soils over most of the Atlantic subregion and is especially common on the coast from New Jersey to Florida; *H. simus* is Austroriparian and chiefly Ocmulgian; while the smallest and most feeble species only, *H. nasicus*, is Sonoran and does not extend west of the Rocky mountains. There is good reason, therefore, to refer *Heterodon* to the Austroriparian, in which case its Neotropical affinity renders it probable that Florida was the region of its origin.

Among Crotalidæ, *Ancistrodon* only can be referred to the Atlantic subregion, *A. contortrix* being spread over its whole extent and *A. piscivorus* confined to the Austroriparian, where numerically it is in excess in the extreme southeast. Both species enter the borders of the Sonoran at suitable localities. The assignment of the genus to the Atlantic coast is further justified by its occurrence in eastern Asia.

Of these more or less cosmopolitan, or Holarctic genera, which must be supposed to have occupied the Nearctic during the Tertiary, and even of related groups restricted to the Nearctic but of sufficient extension there to warrant belief in their relatively considerable age, it is seen that there is reason to believe that all but *Sceloporus, Cnemidophorus, Eumeces, Sistrurus* and *Crotalus* belonged to the Atlantic post-glacial centre, which from the present numerical proportion of species and individuals, as well as the geological age of the region, seems to have been the Ocmulgian.

From this centre a route to the north has been freely open along the low coast plain east of the Alleghenies, to distances into the Eastern district determined for each migrant by limiting conditions, of which, in this case, temperature must be regarded as the most important. A few powerful species, such as *Coluber obsoletus obsoletus, Ophibolus doliatus triangulus* and to a less extent *Pityophis melanoleucus,* have chosen this route to the region north of the Ohio river, turning westward about the Potomac or Susquehanna.

The other main highway was westward along the Gulf coast to the Mississippi river and up that valley, where conditions are highly favorable to reptilian life, spreading eastward at the north to southern Indiana and Ohio. Few species traveled this route unaltered, for with most of them the changed conditions encountered have resulted in the establishing of variations, at least of color, with which a sound taxonomy must reckon. An excellent example of this is *Ophibolus getulus getulus,* which ranges from Florida north to the pine region of New Jersey with no change which has yet been held to warrant a new trinominal, but on its western course, as it enters the Louisianan it becomes *O. g. sayi*, and still further west, in the Texan, is even now perhaps differentiating into a color form known as *O. g. splendidus.* The Louisianan subspecies has moved up the Mississippi valley as far as southern Illinois, and even in that region an occasional specimen shows the pattern of *splendidus.* The lower Mississippi valley may indeed, with some reason, be regarded as a secondary and more modern centre of development in *Chelonia* and *Ophidia.*

Quite different from the condition of temperature which has limited the northward extension of Ocmulgian forms, that which has checked or transformed them on the western route is the lack of moisture encountered beyond the Mississippi, about the beginning of the great plains.

Another northwestward route from the Ocmulgian may have been directly through or around the lower end of the Alleghenies by way of ancient river valleys, but it is not probable that this was traveled as freely as those leading by the coast plain in either direction.

It may be repeated that the present study deals only with post-glacial conditions. If, as has been assumed, the interchange of reptiles between the Nearctic and the Palæarctic was by means of a north Atlantic connection, their Tertiary centres of development were doubtless of greater area and much farther to the north.